

A NEW SPECIES OF *SPHOEROIDES* PUFFERFISH
(TELEOSTEI: TETRAODONTIDAE) WITH
EXTENSIVE HYPEROSTOSIS FROM THE
PLIOCENE OF NORTH CAROLINA

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Abstract.—The relatively intact skull of a tetraodontid pufferfish from the Yorktown Formation (Unit 3 of Lee Creek Mine) of the Pliocene of eastern North Carolina (ca. 5 MYA) represents a new species of *Sphoeroides* from a coastal marine habitat of about 50–80 meters depth. It differs from all of the other species (18 Recent and one fossil) of the genus in the configuration of the bones forming the rim of the upper orbit, the shape of the posterior end of the frontal and the presence of extensive hyperostosis of the opercular bones and ventral postcleithrum. This is the first report of hyperostosis in *Sphoeroides*. With the evidence from the hyperostotic skull, it is reasonable to assume that most of the thousands of previously unidentified, disarticulated, and hyperostotic opercular and cleithral bones that characterize Unit 3 of the Yorktown Formation are the remains of the new species, *S. hyperostosis*. These bones represent specimens ranging in body size from about 80 to 500 mm SL; only four of the 19 other species of *Sphoeroides* reach sizes approaching 250 mm SL.

Skeletal remains, varying from nearly intact whole skeletons to disarticulated parts, of a wide variety of elasmobranch and teleost fish families have been found in Units 1, 2, and 4 basal parts of the Yorktown Formation of the Pliocene of Beaufort County, eastern North Carolina, at Lee Creek Mine. By contrast, Unit 3 of the Yorktown at Lee Creek has few even partial fish skeletons, but a richness of otoliths belonging to 45 taxa in 17 teleost families (Fitch & Lavenberg 1983) and thousands of disarticulated hyperostotic (swollen) bones whose identity has remained a mystery. Some of these hyperostotic bones have been described and illustrated (Weiler 1973), but only with incorrect guesses as to what bones they represent and no identification to taxa other than presumed teleost.

In 1987, a relatively complete skull (Fig. 1) of a tetraodontid pufferfish was recovered by Mr. Craig Healy from Unit 3 at Lee Creek Mine. It has hyperostotic opercular bones

that match the thousands of comparable disarticulated bones from that unit.

Among the approximately 16 genera of tetraodontids surveyed by Tyler (1980), the features of the Pliocene skull are most similar to those found in the speciose genus *Sphoeroides*, especially in: the moderate length and width of the ethmoid; and the anteriorly tapering frontals widely separating the lateral ethmoids and sphenotics, forming the border of the middle of the top of the orbit. The similarity of the Pliocene skull from North Carolina to *Sphoeroides* is not surprising since *Sphoeroides* is one of the two genera of tetraodontids occurring today along the Atlantic coast of North America. The other is *Lagocephalus*, in which the skull has a long posterolateral extension of the frontal contacting the pterotic to roof over a fossa, and a long and broad ethmoid. These specialized features of *Lagocephalus* are not present in the Pliocene skull.

Even while basically similar to *Sphoeroides*, the Pliocene skull differs from those of the 18 extant and the only other fossil species of that genus not only by the presence of hyperostosis, which is absent in all of the other species, but also by the configuration of the lateral ethmoid, frontal, and sphenotic, by the degree that the frontal and sphenotic roof over the posterodorsal region of the orbit, and by uniquely structured posterior flanges of the frontals. This degree of osteological difference between the hyperostotic fossil species and all of the other species is much greater than that between most of the species of relatively similar skull width, but it is about the same degree of difference as that between the species at the ends of the extremes of skull width.

While the presence of swollen, gall-like hyperostotic fish bones has often been considered as a tumorous pathology, we accept current evidence that it is a normal condition in those few species in which it occurs and that it can be species specific in the pattern of bones affected (W. F. Smith-Vaniz, pers. comm. based on manuscript reviewing fish hyperostosis and investigations on the histology and growth of hyperostotic bone). For example, some jacks of the genus *Caranx* that are extremely difficult to distinguish externally exhibit markedly different and consistent patterns of hyperostosis. Therefore, it would be reasonable to describe the Pliocene skull as a new species of *Sphoeroides* on the basis alone of the unique hyperostosis of the opercular bones. Because of our confidence that this hyperostosis is normal and species specific, we name the new species from the Pliocene *Sphoeroides hyperostosis* to call attention to one of its major features of difference from all other species of that genus.

Sphoeroides hyperostosis is known only from the Lee Creek locality that during the Pliocene was a coastal marine habitat estimated to have been of about 50 to 80 m depth (Gibson 1967:646). The skull of *S. hyperostosis* has many general features sim-

ilar to the common northern puffer, *S. maculatus*, that occurs in shallow coastal waters (usually less than 35 m) of the mid-Atlantic states. However, the skull of *S. hyperostosis* also has a few specialized features similar to the more rarely collected blunt-head puffer, *S. pachygaster*, a deeper water (usually more than 100 m) species of almost circumglobal distribution. We hypothesize below on the basis of osteological peculiarities that *S. hyperostosis* is most closely related to *S. pachygaster* and that they together are most closely related to the *S. maculatus-nephelus-parvus-tyleri* species complex defined by Shipp (1974:128–129).

The disarticulated hyperostotic opercular bones that are so common at Lee Creek Mine can reasonably be assumed to be from *S. hyperostosis* because of their similarity to those in the Lee Creek skull. We presume that the disarticulated hyperostotic ventral postcleithra from Lee Creek Mine also are from *S. hyperostosis* simply because it is the only species of *Sphoeroides* (and tetraodontid) known from Lee Creek and the disarticulated ventral postcleithra in general are similar to those of most species of *Sphoeroides*. This assumption is strengthened by the disarticulated ventral postcleithra being relatively broad in the middle region, an unusual feature also found in *S. pachygaster* to which we think *S. hyperostosis* is most closely related.

Methods

The holotypic skull was relatively free of substrate when discovered and was subsequently prepared only to the extent of removing small amounts of substrate from the external surfaces of the exposed bones. The first four vertebrae were attached to the rear of the skull when it was recovered, but the second to fourth vertebrae became detached during preparation. After photographing the skull, with only the first vertebra attached, the premaxilla and dentary from the right side were removed in order to examine the medial surface of these beak-like bones.

Measurements are recorded to nearest 0.1 mm, but given to nearest whole number for measurements over 100 mm. Body length is standard length (SL). Cranial length is from front of palatine to rear of part of cranium formed by exoccipital-epiotic-pterotic to either side of supraoccipital, excluding supraoccipital flange and posterolateral pterotic flange. Interorbital width is least width, just behind lateral ethmoids. Opercle length is from uppermost point on dorsolateral flange above articular head to ventral point. Preopercle length is from anteroventral to posterodorsal points. Subopercle length is greatest anteroposterior distance, not dorsoventral; subopercle thickness is greatest distance between medial and lateral surfaces. Ventral postcleithrum length is between tapering end points above and below. Dentary and premaxillary length is from anteromedially to posterolaterally.

Materials are from the collections of the National Museum of Natural History (USNM), Paleontological Institute, Moscow (PIN), Academy of Natural Sciences of Philadelphia (ANSP), and the Florida State University (FSU).

Analysis of relationships is phenetic and osteological features are considered specialized within *Sphoeroides* if they do not occur in other tetraodontid genera thought to be related to it in this family for which there is no cladistic analysis available.

Materials

Fossil species.—

Sphoeroides jamestyleri Bannikov: PIN 287-9, holotype, 22.6 mm SL, in part and counterpart, Kerch Peninsula, Crimea, southern Ukraine, Tarkhan Horizon, lower Miocene; PIN 3974-8, paratype, ca. 60 mm SL, skull in dorsal view and distorted axial skeleton, single plate; plus uncatalogued piece of caudal skeleton not designated as type material; all with same data as holotype.

Extant species (cleared and stained specimens, unless otherwise noted).—

Sphoeroides angusticeps (Jenyns): ANSP 95841, 1, 172 mm.

Sphoeroides annulatus (Jenyns): ANSP 109459, 3, 15.0–21.4 mm; ANSP 109461, 3, 10.9–15.8 mm; ANSP 109460, 1, 13.5 mm; ANSP 109458, 1, 174 mm.

Sphoeroides dorsalis Longley: ANSP 109462, 1, 131 mm; ANSP 109519, 1, 139 mm (dry skeleton); ANSP 109520, 1, 155 mm (dry skeleton).

Sphoeroides formosus (Günther): ANSP 95552, 1, 175 mm (often recognized in the monotypic genus *Guentheridia*).

Sphoeroides georgemilleri Shipp: ANSP 117319, 1, 88.4 mm (paratype).

Sphoeroides greeleyi Gilbert: ANSP 109463, 3, 24.2–60.8 mm.

Sphoeroides lobatus (Steindachner): ANSP 97332, 1, 67.5 mm.

Sphoeroides maculatus (Bloch & Schneider): ANSP 109466, 1, 126 mm; ANSP 109464, 2, 97.5–106 mm; ANSP 109467, 1, 201 mm. Dry skeletons: ANSP 16793, 1, 172 mm; ANSP 109552, 1, 171 mm; USNM 283611, 1, 205 mm; USNM 163742, 1, 188 mm; USNM 12986, 1, 172 mm; USNM 273171, 1, 139 mm. Alcohol preserved (top of skull examined with skin laid aside): USNM 75162, 1, 225 mm; USNM 42481, 1, 210 mm; USNM 75161, 1, 206 mm; USNM 315196, 2, 169–182 mm; USNM 93847, 1, 174 mm; USNM 14827, 2, 153–175 mm; USNM 42476, 1, 110 mm; USNM 25689, 1, 147 mm; USNM 28750, 1, 150 mm; USNM 163742, 1, 157 mm; USNM 50891, 1, 160 mm; USNM 51869, 1, 171 mm; USNM 74873, 1, 161 mm; USNM 61468, 2, 122–142 mm; USNM 156489, 2, 87.2–110 mm; USNM 315195, 4, 74.5–101 mm. Radiographs: USNM 75162, 1, 225 mm; USNM 42481, 210 mm; USNM 75161, 1, 206 mm; USNM 315196, 2, 169–181 mm; USNM 14827, 2, 153–175 mm; USNM 93847, 1, 174 mm; USNM 28750, 1, 150 mm; USNM 25689, 1, 147 mm; USNM 42476, 1, 110 mm; USNM 4638, 4, 74.3–184 mm; USNM 156489, 2, 86.7–109 mm; USNM 156477, 2, 63.5–78.4 mm;

USNM 118348, 5, 66.2–108 mm; USNM 155996, 1, 78.6 mm; USNM 156478, 1, 85.3 mm; USNM 156523, 1, 64.1 mm; USNM 155988, 1, 125 mm; USNM 91107, 1, 132 mm; USNM 155843, 1, 122 mm; USNM 36016, 1, 98.7 mm; USNM 143012, 5, 25.1–34.6 mm.

Sphoeroides marmoratus (Lowe): ANSP 106505, 1, 98.4 mm.

Sphoeroides nephelus (Goode & Bean): ANSP 105222, 1, 48.5 mm; ANSP 110533, 1, 128 mm.

Sphoeroides pachygaster (Müller & Troschel): Cleared and stained: ANSP 109468, 2, 134–137 mm; ANSP 104781, 1, 117 mm; ANSP 101322, 1, 80.6 mm. Alcohol preserved (top of skull examined with skin laid aside): USNM 42143, 1, 218 mm; USNM 121952, 1, 159 mm; USNM 307615, 1, 129 mm; USNM 307615, 1, 127 mm. Radiograph: USNM 42143, 1, 218 mm.

Sphoeroides parvus Shipp & Yerger: USNM 120084, 2, 38.7 and 80.3 mm. Radiographs: USNM 203248, 1, 79.7 mm (holotype); USNM 156492, 3, 62.8–84.9 mm.

Sphoeroides sechurae Hildebrand: USNM 128123, 1, 56.3 mm (paratype).

Sphoeroides spengleri (Bloch): Dry skeletons: ANSP 10531, 1, ca. 90 mm; ANSP 10532, 1, 92.8 mm.

Sphoeroides testudineus (Linnaeus): ANSP 107328, 1, 68.5 mm.

Sphoeroides trichocephalus (Cope): ANSP 109742, 1, 57.1 mm.

Sphoeroides tyleri Shipp: USNM 227198, 2, 51.6 and 73.4 mm.

Sphoeroides yergeri Shipp: FSU 25256, 1, 59.5 mm (paratype).

Lagocephalus inermis (Temminck & Schlegel): ANSP 100832, 1, 52.2 mm. Radiograph: USNM 207052, 1, 334 mm.

Lagocephalus laevigatus (Linnaeus): ANSP 103120, 1, 61.4 mm; ANSP 102155, 2, 143–166 mm. Dry skeleton: ANSP 102154, 1, ca. 290 mm. Wet disarticulated skeleton: ANSP 102153, 1, ca. 290 mm. Radiographs: USNM 120066, 1, 232 mm; USNM 37689, 1, 279 mm; USNM 76680,

1, 329 mm; USNM 22807, 1, 386 mm; USNM 20757, 2, 145–148 mm; USNM 156515, 1, 121 mm; USNM 15632, 1, 112 mm; USNM 156531, 1, 118 mm; ANSP 207052, 1, 334 mm; ANSP 78225, 1, 419 mm; ANSP 78235, 1, 312 mm; ANSP 102154, 1, ca. 300 mm.

Lagocephalus lagocephalus (Linnaeus): ANSP 70299, 1, 214 mm.

Lagocephalus lunaris (Bloch & Schneider): ANSP 111509, 1, 62.3 mm.

Lagocephalus scleratus (Gmelin): ANSP 96685, 1, 80.9 mm.

Lagocephalus spadiceus (Richardson): ANSP 104787, 1, 98.2 mm.

Tetraodontidae (sensu Tyler, 1980)

Sphoeroides Anonymous (Lacepède, 1798) (as defined by Fraser-Brunner 1943, Shipp & Yerger 1969, Shipp 1974, Tyler 1980, and Tyler & Paxton 1979).

Sphoeroides hyperostosus, new species

Type specimens and horizon.—USNM 437601, holotype, relatively complete skull and first four vertebrae, 72.5 mm cranial length, original number 378527, Lee Creek Mine, Aurora, Beaufort County, North Carolina, Unit no. 3 of the Yorktown Formation, lower Pliocene, about 5 MYA, collected 5 December 1987 by Craig Healy; USNM 290643, paratype, incomplete cranium, 37.0 mm greatest length, same locality as holotype. All of the following are disarticulated hyperostotic bones in the USNM Lee Creek Osteichthyes collection, most of which are uncatalogued. Most of the catalogued pieces are in the 283, 288 and 440 thousand series. All bones illustrated here have been catalogued. The four most common disarticulated bones in the collection referable to *S. hyperostosus* but not designated as type specimens are: 1047 ventral postcleithra, 19.7 to 70.8 mm; 734 subopercles, 12.1–39.6 mm; 712 preopercles, 18.5–56.5 mm; 211 opercles, 16.4–40.6

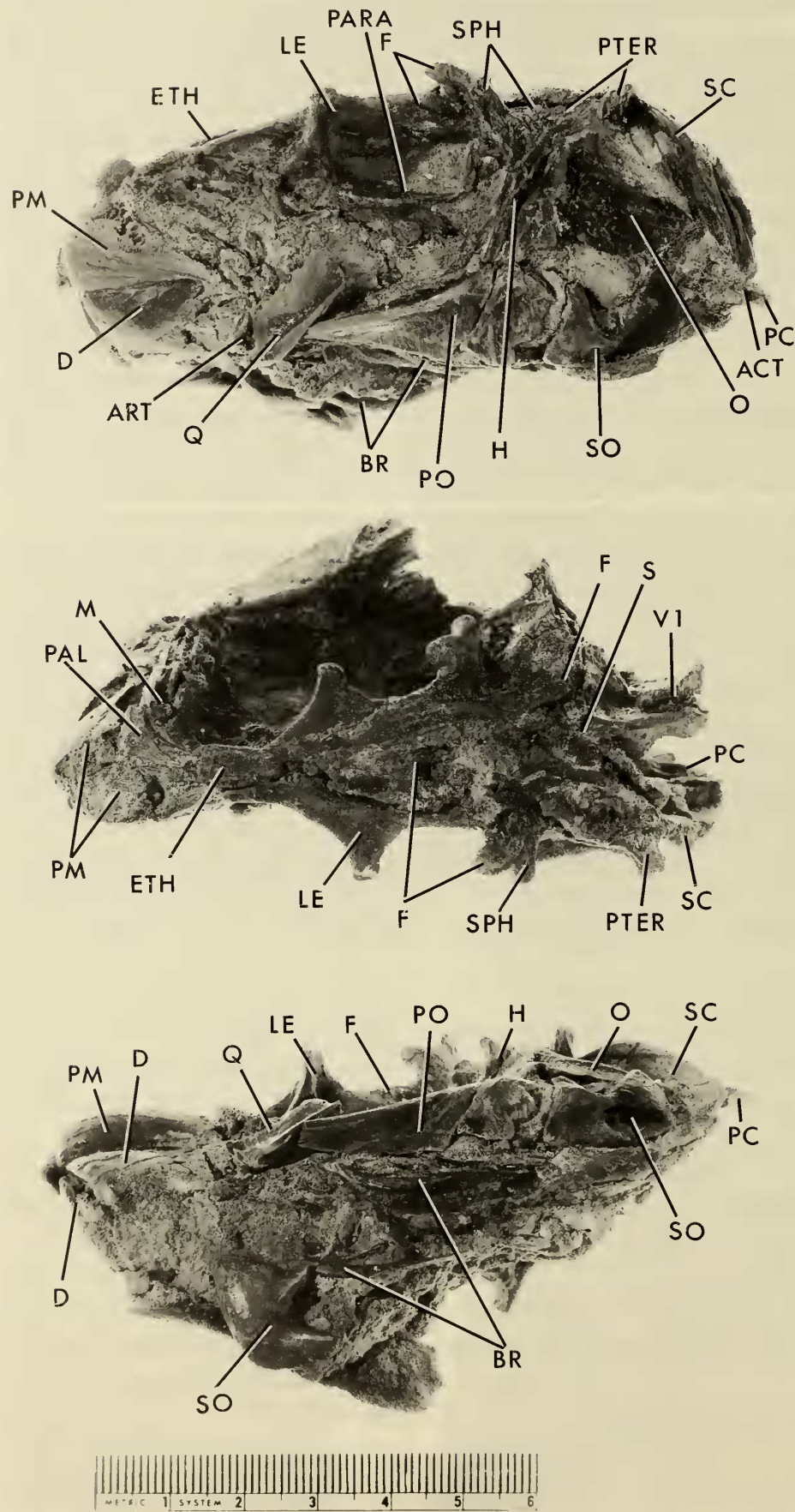


Fig. 1. *Sphoeroides hyperostosus*, USNM 437601, holotype, Pliocene of the Yorktown Formation, Lee Creek Mine, North Carolina, 72.5 mm cranial length, lateral (above), dorsal (middle) and ventral (below) views of the skull, representing a fish of about 240 mm SL. Abbreviations for the names of the bones here and in other

mm. Additionally, there are 8 dentaries, 19.6–27.7 mm, and 7 premaxillae, 17.3–30.4 mm.

Etymology. — *Hyper*, a great amount, and *ostosus*, bony growth; for the normally swollen bones; masculine.

Diagnosis. — Differs from all other species of *Sphoeroides* by the: hyperostosis of the opercle, subopercle, preopercle, and ventral postcleithrum; lateral ethmoid with a broad flat unornamented upper surface, without an obliquely sloping anteroventral edge, the flange formed by the frontal and sphenotic at the posterodorsal region of the orbit directed anterolaterally, increasing the amount of roofing over the orbit; the posterior region of the dorsal surface of the frontal with a thick curved crest that extends posteriorly as a short process over the epiotic.

Description. — Most of the bones of the skull of the holotype (Fig. 1) are present on one side or the other. On the left (more complete) side of the skull the only bone missing is the maxilla. The maxilla is present, however, on the right side. The pectoral girdle on the left side is represented by the supracleithrum, dorsal postcleithrum, some of the actinosts and the dorsal region of the coracoid-scapula, and, internal to the latter and not exposed in lateral view, the cleithrum (which can be seen clearly in medial view). The pterygoid series is present on both sides but the limits of the individual bones are unclear. The branchiostegal rays are present on the left side, with the enlarged first ray that forms the specialized tetraodontid pumping plate well exposed. The opercular series is missing from the right side, as is the pectoral girdle except for some pieces of the cleithrum. The pterotic on the right side is displaced forward.

The roof of the skull is distorted by a longitudinal fracture along much of the length of the frontal and ethmoid on the left side. The portions of the skull to either side of the fracture are slightly separated from one another and slightly displaced antero-posteriorly relative to one another. The amount of separation, displacement, and artificial widening of the skull has been taken into account and adjusted for in the dorsal view reconstruction of the skull and in the measurement of the interorbital width.

The paratypic skull (Fig. 2) is far less complete and much abraded. It represents the top of the neurocranium, with the rear portion missing, the lateral processes of the lateral ethmoids abraded, especially on the left side, the front of the ethmoid-vomer missing, the frontals incomplete posteriorly, the lateral processes of the frontal and sphenotic in the posterodorsal region of the orbit abraded, and most of the supraoccipital and epiotic region, along with the pterotic, missing. The greatest length of the incomplete cranium is 27.0 mm. What remains of the top of the cranium of the paratype is entirely consistent with the structure in the larger and better preserved holotype, including a comparable interorbital width (13.7 mm) relative to the approximate length and width of the cranium. The descriptions of the skull that follow are based on the holotype unless otherwise stated.

The upper and lower jaws (Figs. 1 and 4) are typical for a tetraodontid, and a single rounded trituration or internal mastication tooth is present posteromedially on the inner surface of each premaxilla. The palatine broadly interlocks with the vomer medially and posteriorly, whereas the vomer underlies the anterior region of the ethmoid, which

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figures: ACT—actinost; ART—articular; BR—branchiostegal ray; D—dentary; ETH—ethmoid; EO—exoccipital; EPI—epiotic; F—frontal; H—hyomandibula; IO—interopercle; LE—lateral ethmoid; M—maxilla; O—opercle; PAL—palatine; PARA—parasphenoid; PC—postcleithrum (dorsal); PM—premaxilla; PO—preopercle; PTER—pterotic; Q—quadrate; S—supraoccipital; SC—supracleithrum; SPH—sphenotic; SO—subopercle; V—vomer; V1—first vertebra.



Fig. 2. *Sphoeroides hyperostosis*, USNM 290643, paratype, Pliocene of the Yorktown Formation, Lee Creek Mine, North Carolina, 37.0 mm greatest length of the much abraded incomplete cranium; dorsal view to left, ventral view to right.

is of moderate width. The lateral ethmoids are robust and have a broad flat upper surface without an obliquely sloping anterolateral region to accommodate the nasal apparatus; rather, the flat anterolateral edge extends out as a roof over this area.

The frontals taper to an indistinct point in the region between the anterior ends of the dorsal surface of the lateral ethmoids. The frontals are somewhat upraised where they form the lateral margin of the middle of the upper region of the bony orbit, widely separating the lateral ethmoids and sphenotics. Just behind the orbit the frontal and sphenotic form a strong laterally and slightly anteriorly directed process. This process

increases the amount of roofing over the posterodorsal region of the orbit and decreases the distance between the frontal-sphenotic flange and the lateral wing of the lateral ethmoid. The upraised interorbital margin of the frontal continues posteriorly as a thick ridge that curves medially to the region in front of the supraoccipital and then curves posterolaterally to form a process that extends out slightly above the epiotic as a short narrow roof over the anterodorsal region of that bone.

The pterotic has a strong lateral process in the region between its articulation with the hyomandibula and supracleithrum. The limits of the anterior region of the supraoc-

cipital between the posterior flanges of the frontals are indistinct, but the supraoccipital crest is well preserved, projecting posteriorly between the bifid neural arch of the first vertebra. The supracleithrum is robust, with a laterally expanded posterior edge and a thinner anterior flange. The dorsal postcleithrum, expanded in the middle and tapering at both ends, articulates anterodorsally along the medial surface of the upper end of the cleithrum (not exposed in lateral view), whereas its posteroventral end (only slightly exposed in lateral view), which would articulate with the missing ventral postcleithrum, lies just behind the region of the indistinct remains of the hour glass-shaped actinosts and coracoid-scapular complex.

The opercle is slightly hyperostotic, about as much so as most of the disarticulated opercles from Lee Creek. The dorsal end of the opercle forms a head for articulation with the upper posterior edge of the hyomandibula, while the opercle is incomplete ventrally where it would overlie the subopercle.

The subopercle is moderately hyperostotic, less so than most of the disarticulated subopercles of comparable size, but with about the same degree of swelling as in the three bones numbered 364322, 364227 and 440859 in Fig. 3. The posterodorsal lobe of the subopercle behind the dorsal indentation for articulation with the opercle is slightly longer and has a more oblique edge facing the ventral flange of the opercle than is the case with the anterodorsal lobe, whereas the anteroventral edge of the subopercle is more acute than the rounded posteroventral edge. The groove on the subopercle at the bottom of its dorsal indentation to accommodate the opercular flange is on the lateral surface. These asymmetries are useful in determining which of the disarticulated subopercles are from the left versus right side of the skull.

The hyomandibula has a sturdy upper portion of triangular shape in lateral view

for articulation with the cranium (sphenotic in front and pterotic behind in lateral view) and a lower shaft-like portion, demarked from the upper by a thick crest horizontally along its surface, supporting the dorsal region of the opercle. The preopercle is moderately hyperostotic, less so than most of the disarticulated preopercles of comparable size, but with about the same degree of swelling as in the largest of the preopercles in Fig. 3. The preopercle is much fractured but has an entirely normal tetraodontid shape and articulation along the ventral shaft of the hyomandibula and ventral edge of the quadrate.

The quadrate is displaced anteroventrally but obviously when complete had a typical tetraodontid shape and articulation with the preopercle posteroventrally, the pterygoid bones dorsally and the articular anteriorly. The limits of the pterygoid bones are not well preserved, but everything that is evident is typical of tetraodontids and *Sphoeroides*, including a large, posteriorly rounded metapterygoid and a vertically oriented mesopterygoid contacting the region of articulation between the vomer and lateral ethmoid. The remains of a rod-like interhyal are evident behind the fractured and displaced regions of the quadrate and anterior end of the preopercle.

The parasphenoid is a strong shaft under the orbit; its ventral flange is not exposed. Anteriorly the parasphenoid supports the thick ventral shaft of the lateral ethmoid, while posteriorly its dorsolateral flanges meet the prootics. The prootics have medial flanges forming a partial roof over at least the anterior region of the myodome. The parasphenoid lacks a dorsal lobe in the interorbital septum that in some tetraodontids contacts the frontals.

Measurements of the holotype are: cranial length 72.5 mm; least interorbital width 15.2 mm when corrected for fracture (interorbital width into cranial length $4.8\times$); supracleithrum length 30.4 mm; subopercle length, horizontally from anterior to pos-

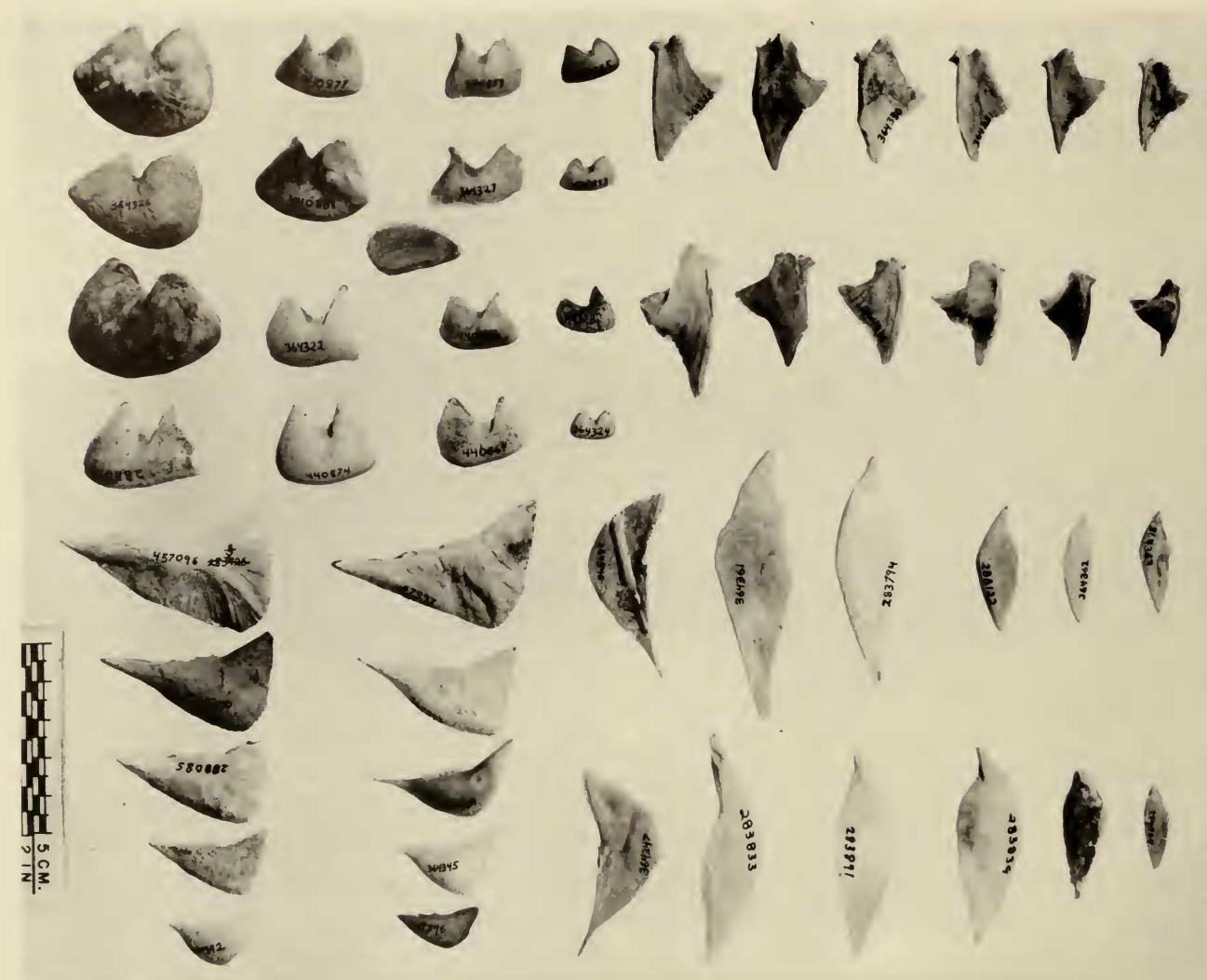


Fig. 3. *Sphoeroides hyperostosus*, a selection of disarticulated hyperostotic bones from Lee Creek Mine, showing most of the range in size and variation in degree of hyperostosis. All bones in lateral view unless otherwise stated. Upper left, subopercles: upper two horizontal rows, left side; lower two horizontal rows, right side; in middle, a section through middle of horizontal length of one of the subopercles; range in horizontal length 12.1 to 39.6 mm. Lower left, preopercles: two vertical rows to left, left side; two bones to right, medial view of left (above) and right preopercles to show interopercle in place on bone above and shallow groove to accommodate it on bone below; range in length from anteroventral to posterodorsal ends 22.3 to 54.0 mm. Upper right, opercles: upper horizontal row, left side; lower horizontal row, right side; range in greatest length 16.4 to 40.6 mm. Lower right, ventral postcleithra: upper horizontal row, left side; lower horizontal row, right side; range in greatest length 22.0 to 70.5 mm.

terior 18.5 mm; preopercle length, from posterodorsal end to estimated anterior end 55.0 mm; opercle length, from dorsal end to estimated ventral end 26.7 mm; ethmoid region width (ethmoid and vomer combined) 6.8 mm when corrected for fracture; distance between lateral edge of left pterotic and midline of cranium 22.4 mm, therefore about 45 mm greatest width of cranium when corrected for displaced right pterotic; greatest width between lateral edges of lat-

eral ethmoids 29.8 mm when corrected for fracture; greatest width between anterolateral flanges of sphenotics at rear of orbit 37.0 mm when corrected for fracture; distance between rear edge of extreme lateral end of lateral ethmoid and front edge of anterolateral process of frontal (and sphenotic) at rear of orbit 11.5 mm on right side and 12.3 mm on left, average 11.9 mm.

To obtain an estimate of the standard length of the fossil fish represented only by

the skull with a 72.5 mm cranium, measurements comparable to those above were taken on the five largest dried skeletons of *S. maculatus* available to us: 171 to 205 mm SL, which have slightly smaller crania, 49.3 to 58.8 mm, than that of *S. hyperostosis*. *Sphoeroides maculatus* was used in this comparison rather than *S. pachygaster* or some other species simply because of the availability of a far greater number of large specimens of *S. maculatus* either preserved in alcohol or as skeletal preparations on which we could record skull measurements than of *S. pachygaster* (several test extrapolations based on *S. pachygaster* give approximately comparable results to those based on *S. maculatus*). Three of these measurements of *S. maculatus* that are relatively long and amenable to precise measurement for the five largest dried skeletons are, as averages: length of cranium 30.3% SL; length of supracleithrum 12.7% SL; length of preopercle 23.0% SL. Using the same measurements from the fossil skull and extrapolating from those of the five specimens of *S. maculatus* of 181 mm average SL gives an estimated size for *S. hyperostosis* of 245 mm SL based on the length of the cranium, 236 mm SL based on the length of the supracleithrum, and 239 mm SL based on the length of the preopercle. We use the average figure of 240 mm SL as the best estimate of the length of the specimen represented by the holotypic skull.

Since some of the thousands of disarticulated hyperostotic bones (Fig. 3) at Lee Creek are substantially larger or smaller than those of the fossil skull, we have measured the size range of each of the four most common kinds (see Materials) to estimate the length of the fish they represent based on extrapolations from *S. maculatus*. The relative lengths of these bones are not subjected to much allometric change and we have therefore used simple extrapolations rather than regression coefficients that would have required a much more exhaustive survey of *S. maculatus*. In addition to the figure

given above for the preopercle, the five dried skeletons of *S. maculatus* have an average opercle length (vertical) of 11.1% SL, subopercle length (horizontal) of 7.7% SL, and ventral postcleithrum length of 20.6% SL. Employing these figures from the 181 mm average SL specimens of *S. maculatus*, the disarticulated and hyperostotic bones that dominate Unit 3 at Lee Creek represent specimens of *S. hyperostosis* of 95 to 340 mm SL based on the 1047 ventral postcleithra, 157 to 513 mm SL based on the 734 subopercles, 81 to 246 mm SL based on the 712 preopercles, and 147 to 364 mm SL based on the 211 opercles. The fewer non-hyperostotic and disarticulated bones (Fig. 4) of *S. hyperostosis* from Lee Creek have dimensions indicating that they represent specimens within the above size ranges.

Of this estimated size range of 81 to 513 mm SL, we qualify the 513 mm SL figure based on the largest subopercle. The subopercles are the most extensively swollen of the hyperostotic bones, and, whereas most of the swelling is accommodated by mediolateral expansion, a small amount of swelling also probably involves an increase in the anteroposterior dimension of the subopercle. Therefore, we reduce the maximum size figure based on the subopercles and estimate it to be about 500 mm SL.

As an example of the enormous increase in thickness of the hyperostotic bones as seen especially in the subopercle, the largest disarticulated subopercle of *S. hyperostosis* is 39.6 mm in horizontal length and 18.4 mm in mediolateral thickness (thickness 46% of length), whereas in a somewhat smaller but slightly more swollen subopercle the length is 34.2 mm and the thickness 16.9 mm (thickness 49% of length). By contrast, the non-hyperostotic subopercles in the dried skeletons of *S. maculatus* are wafer thin (thickness 4 to 6% of length), even including the strengthening ridges along the lateral surface radiating out from the groove for articulation with the opercle. Among the disarticulated opercular bones are an oper-



Fig. 4. *Sphoeroides hyperostosus*, a selection of non-hyperostotic bones from Lee Creek Mine. Upper row, premaxillae, those on the left from the right side and those to the right from the left side, greatest length of most intact bone (364351) 30.4 mm. Middle row, dentaries, the two on the left from the right side and that to the right from the left side, the bone numbered 437601 and the premaxilla above it of the same number removed from the holotype, greatest length of most intact bone (364356) 27.7 mm. Lower row, from left to right: second to fourth abdominal vertebrae removed from the holotype, 26.5 mm greatest length along middle of centra, lateral view; left and right palatines, greatest length 28.4 mm, obliquely lateral view; two vomers, greatest length 24.9 mm, dorsal view.

cle and subopercle that are firmly attached to one another by their hyperostosis (Fig. 5). There are no non-hyperostotic examples of tetraodontid opercular bones among the Lee Creek collections.

Comparisons

The general configuration of the bones of the holotypic fossil skull has been compared

to that in the other genera of tetraodontids, as described and illustrated by Tyler (1980: 313–324, figs. 226, 227, 245, 257–261). The fossil is most similar to *Sphoeroides*, especially as seen in the proportions of the ethmoid and the configuration of the frontals where they separate the lateral ethmoids anteriorly and the sphenotics more posteriorly. The major osteological features that

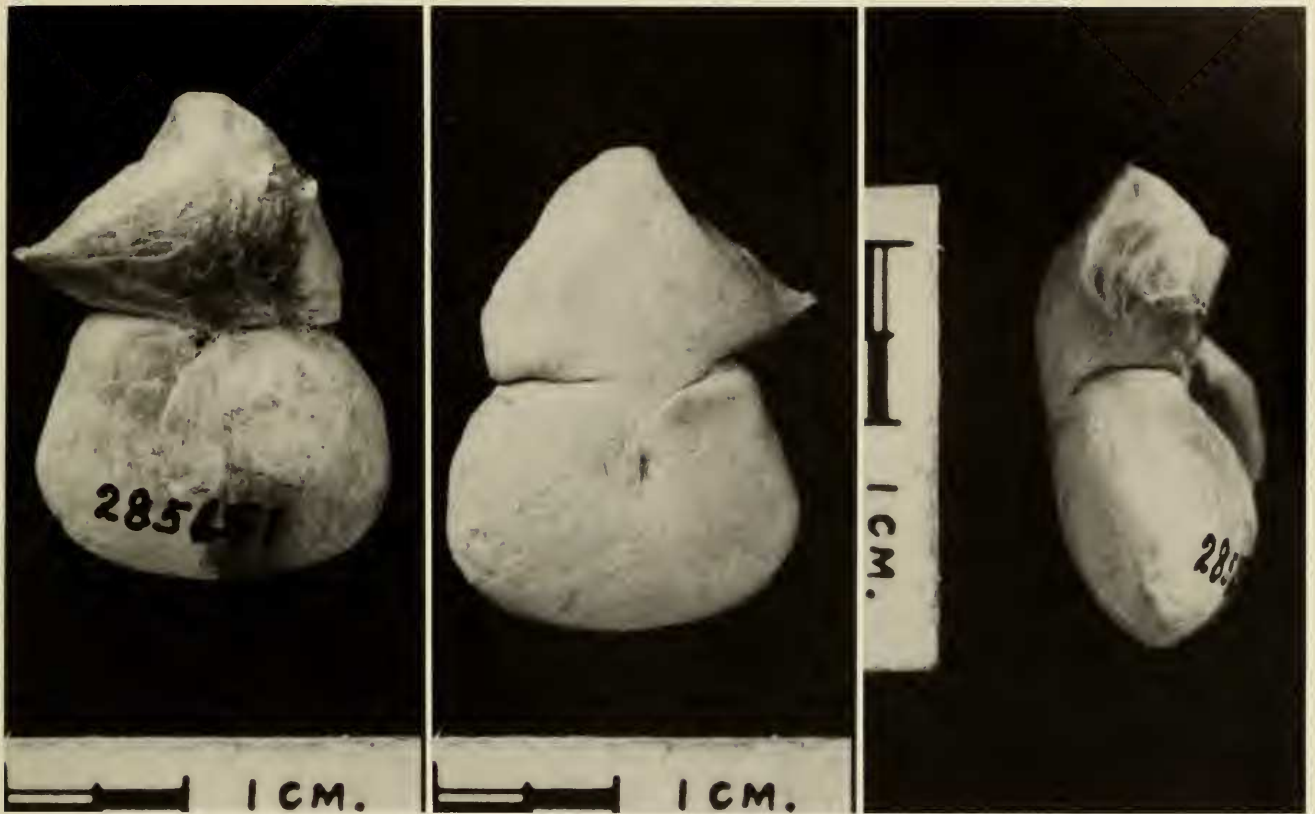


Fig. 5. *Sphoeroides hyperostosis*, USNM 285651, an opercle (above; much abraded dorsally) and subopercle from the left side held tightly together by hyperostosis; medial view to left, lateral view in middle, and posterior view to right to show the thickness of the bones; greatest vertical length of the two bones together 27.3 mm; greatest horizontal length, that of the subopercle, 19.1 mm; greatest thickness, that of the subopercle, 10.8 mm.

distinguish *Sphoeroides* from the genera most closely related to it (*Lagocephalus*, *Pelagocephalus*, *Takifugu*, *Torquigener* and *Amblyrhynchotes*) have been summarized by Tyler & Paxton (1979). Unfortunately, only a few of these are features that can be seen in the holotypic fossil skull, but those three that can be determined are consistent with its placement in *Sphoeroides*: there are trituration teeth in the upper jaw (at least one tooth present); there is no dorsal flange of the parasphenoid in the orbit; and there are well-developed remnants of the anterior edge of the dorsal roof of the myodome. Since the holotypic skull is closest in form to that of *Sphoeroides*, we analyze below those features that distinguish it from all of the other species of *Sphoeroides* and those that indicate its relationships within that genus.

Within *Sphoeroides* the single most important cranial character that is likely to be seen in a fossil and to be a reliable indicator

of at least general relationships is the width of the interorbital. The 12 Atlantic species have been systematically redescribed and phenetically related mostly on the basis of external characters by Shipp (1974). Shipp gives data on the interorbital width for each species. These measurements were obtained by calipers externally through the skin, but they were taken with such firm pressure of the skin against the bone that Shipp's measurements are equivalent to ours made on skeletal material (R. L. Shipp, pers. comm.). For example, Shipp (1974:140) gives the range and mean of the least interorbital width for 20 specimens of *S. maculatus* of 83–217 mm SL as 5.0–7.0% SL (aver. 5.8), whereas our measurements for 29 specimens of *S. maculatus* of 75–225 mm SL are 4.6–6.6% SL (5.8), with width into cranial length figures of 4.5–5.5 times (5.0). For another species discussed below, *S. pachygaster*, Shipp (1974:138) gives the interorbital width as 6.2–12.2% SL (8.7) and especially

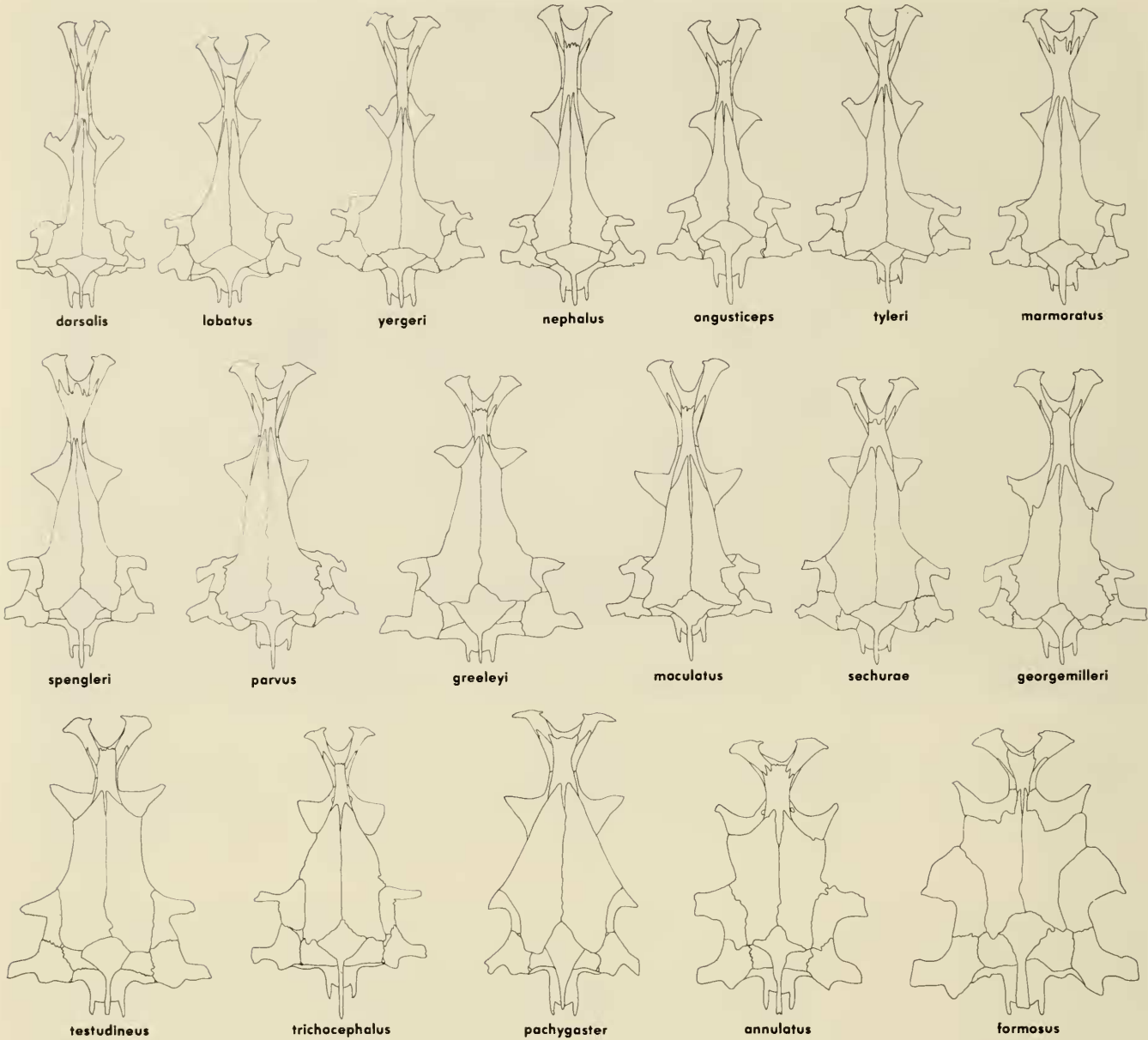


Fig. 6. Outlines of dorsal views of the skulls in the 18 extant species of *Sphoeroides*, to show the variation in interorbital width in this genus from extremely narrow to extremely broad.

variable in 20 specimens of 90–188 mm SL, with which our eight specimens agree. Tyler (1980) treated the osteology and phenetic relationships of 12 species of *Sphoeroides*, including five of the six eastern Pacific species, and illustrated dorsal views of the skull from which interorbital width can be obtained for all 12 species. For present purposes we have examined and illustrated in dorsal view the skulls of the six extant species of *Sphoeroides* not treated by Tyler, including the only species not treated by either Shipp or Tyler, *S. sechurae* from the eastern Pacific, so that the skulls of all 18 extant

species may be more easily compared here (Fig. 6).

Interorbital width, expressed in this survey as the average number of times the least bony interorbital width is contained in the cranial length, is exceptionally diverse in *Sphoeroides*, more so than in any other speciose genus of tetraodontids (e.g., width is remarkably similar in all of the 23 species of *Canthigaster*). The least interorbital width in adults of the 18 extant species of *Sphoeroides* ranges from: extremely narrow (about 10.5 times in cranial length) in *lobatus*, *yergeri*, and *dorsalis*; to relatively narrow (6.5

to 9.0) in *angusticeps*, *marmoratus*, *nephelus*, and *tyleri*; to moderate (4.0 to 6.0) in *georgemilleri*, *greeleyi*, *maculatus*, *parvus*, *sechurae*, *spengleri*, and *testudineus*; to relatively broad (3.0 to 3.5) in *pachygaster* and *trichocephalus*; and to extremely broad (2.0 to 2.5) in *annulatus* and *formosus*. In the only previously described fossil species of *Sphoeroides*, *S. jamestyleri* Bannikov (1990) from the Miocene of the Crimea (southern Ukraine), the interorbital is relatively narrow, 7.1 times in cranial length.

We do not attempt a cladistic analysis here because we have only gross skull characters for *S. hyperostosus* and none of the numerous external body characters useful in recognizing at least phenetic groups within the Recent species of *Sphoeroides*, which have not been analyzed cladistically. However, we note that a moderate to relatively broad interorbital is generalized in tetraodontids, for that is the adult condition in most of the other genera of both of the subfamilies (tetraodontins and canthigasterins) of the Tetraodontidae and in the Triodontidae (least interorbital 2.5 times in cranial length), the most morphologically generalized family of extant tetraodontoids (triodontids being the sister group of all of the other extant families of tetraodontoids—the tetraodontids, diodontids, and molids). Moderate interorbital width also is the condition in the Triacanthodidae (4.0), the most morphologically generalized tetraodontiform family, whereas the interorbital is much broader in the Molidae (2.0) and greatly increased in width in the Diodontidae (1.0). The interorbital width is unknown in the Eocene Eoplectidae, which is the most morphologically generalized family of tetraodontoids and the sister group of all of the extant families of that group (in Tyler & Patterson 1991:878, the first author by *lapsus calami* reversed the relationship of the Eoplectidae and Triodontidae).

In *S. hyperostosus* the least interorbital width is moderate, contained 4.8 times in the cranial length (or 6.3% SL based on the

extrapolated 240 mm SL). Of the seven extant species of *Sphoeroides* with a moderate interorbital, *S. hyperostosus* has a skull structure relatively similar to that of *S. parvus* and *S. maculatus*, which have interorbital widths of 5.5 and 5.0 respectively. *Sphoeroides parvus* and *S. maculatus* are believed to be very closely related within a complex of four species, the other two of which, *tyleri* and *nephelus*, have narrower interorbitals of 8.0 and 9.0 respectively (Shipp 1974:128–129). All four of these are western Atlantic species, and two of them, *maculatus* and *nephelus*, occur along the Atlantic coast of the United States. It might be expected that *S. hyperostosus* from the Pliocene of coastal North Carolina would be most closely related to one of these two, especially to *maculatus*, which has a similar interorbital width, rather than to *nephelus*, which has a narrower interorbital. We note that there is no assurance that *S. hyperostosus* was confined to the Atlantic coast of the United States and since its one locality of collection is a relatively deep water habitat it is possible that, like *S. pachygaster* discussed below, it was far more widely distributed.

These general features of similarity, including the generalized interorbital width, between the skull of *S. hyperostosus* and those of *S. maculatus* from the Carolinas and *S. parvus* from the Gulf of Mexico, cannot be used to establish how closely they might be related. However, the several unusual features of the skull (Fig. 7) that distinguish *S. hyperostosus* from the members of the complex that includes *S. maculatus* are comparable to specializations found in the deep water *S. pachygaster* of nearly circumglobal distribution, as follows.

In *S. hyperostosus* the dorsal surface of the lateral ethmoid is flat and smooth, and lacks an anteroventrally sloping surface in the anterior region. The flat anterolateral region of the upper surface of the lateral ethmoid forms a narrow shelf over the region of the olfactory apparatus. No other

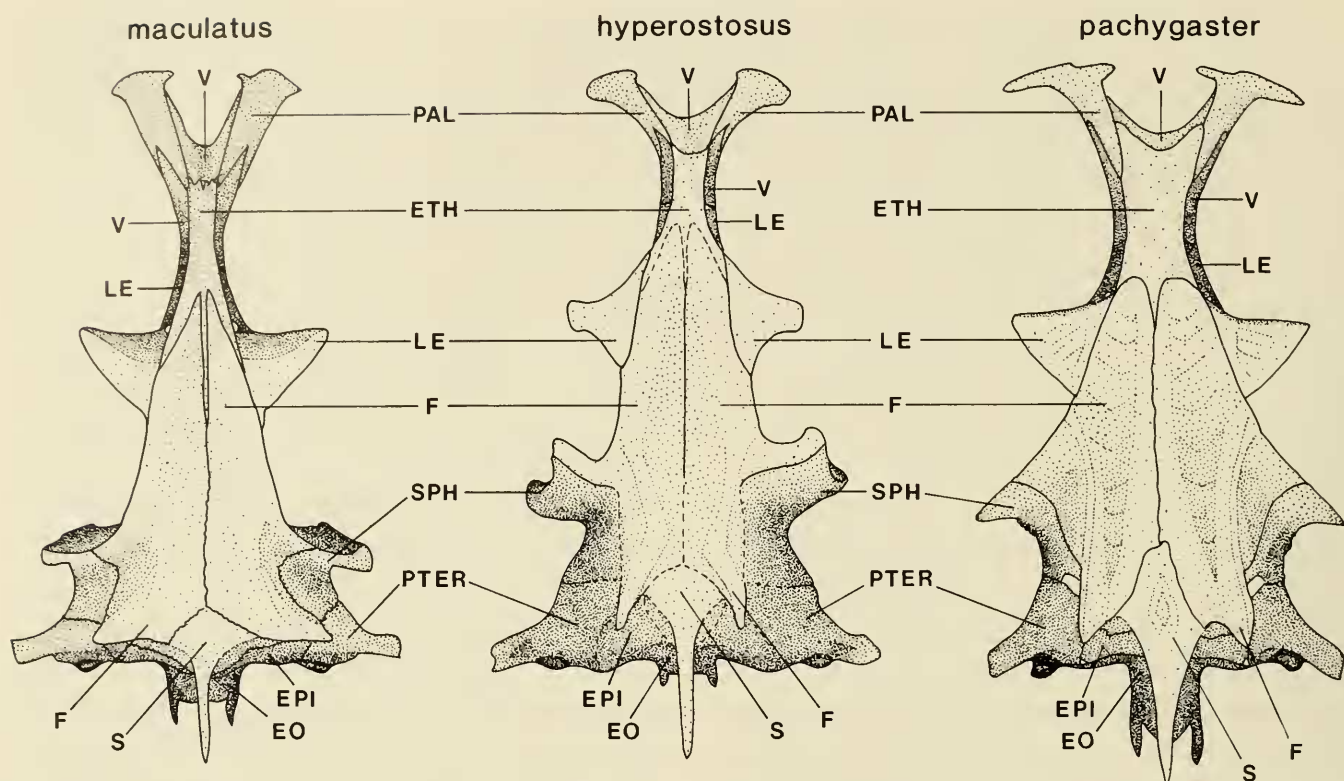


Fig. 7. Dorsal view of the skull of *Sphoeroides hyperostosus* (USNM 437601, ca. 240 mm SL) in comparison to those of *S. maculatus* (ANSP 109517, 179 mm SL) and *S. pachygaster* (ANSP 104781, 117 mm SL); the skull of *S. hyperostosus* reconstructed with correction for the distortion associated with the fracture along the left side of the frontal and ethmoid.

species of *Sphoeroides* has such a flat upper surface to the lateral ethmoid, nor a shelf over the olfactory region. Rather, all the other species of *Sphoeroides* have some degree of oblique anteroventral slope to the front edge of the lateral ethmoid (for extant species see Tyler 1980, figs. 257–262), as is also the case in the genera considered closely related to *Sphoeroides*.

However, the oblique slope is least developed in *S. pachygaster*, and in some specimens the slope is essentially absent (Fig. 7 shows the average condition of a slight oblique slope), and the anteroventral edge of the prefrontal in *S. pachygaster* does not form such a definite shelf over the olfactory region as in *S. hyperostosus*. Thus, in the shape of its lateral ethmoid, *S. hyperostosus* is most similar to *S. pachygaster* among all of the species of the genus. Nevertheless, the dorsal surface of the lateral ethmoid, and of the frontals, in *S. pachygaster* differs from all other species of *Sphoeroides* in be-

ing deeply and delicately sculptured by crests and grooves, and in being only weakly ossified, with the frontals sometimes having cartilaginous edges (Shipp 1974:127, Tyler 1980:319).

In *S. hyperostosus* the posterodorsal region of the orbit is bounded by a strong laterally and somewhat anteriorly directed process formed by the frontal (anteriorly) and sphenotic (posteroventrally). In most other species of *Sphoeroides*, including the Miocene *S. jamestyleri* and all the extant species with moderate or only somewhat wider or narrower interorbitals, only the posterior wall of the orbit is bounded by a lateral process. Moreover, when present this process is formed by the sphenotic alone, without the involvement of a strong process from the frontal at about a right angle to the rest of the bone, as in *S. hyperostosus*. In the two species of *Sphoeroides* with extremely broad interorbitals, *S. annulatus* and *S. formosus*, the sphenotic is expanded lat-

erally and in one case (*formosus*) anteriorly as well, over the rear of the upper orbit. However, in these two species the sphenotic expansion is associated with the general broadening of the skull and differs from the condition in *S. hyperostosis* by not involving a lateral process of the frontal and not forming a strong thick process over just the posterodorsal region of the orbit.

The only configuration of the bones at the upper rear of the orbit comparable to that in *S. hyperostosis* is found in *S. pachygaster*. The frontals in *S. pachygaster* broaden posteriorly over the orbit in a relative straight line behind the lateral ethmoids and meet prominent anterolaterally directed processes from the sphenotics that roof over the posterolateral region of the orbit. While the contribution to this roofing by the frontal is not as distinctively at a right angle to the longitudinal axis of the frontal as in *S. hyperostosis*, the prominent contribution in *S. pachygaster* of an anterolaterally oriented part of the sphenotic is distinctive and similar to that in *S. hyperostosis*, more so than to any other species of *Sphoeroides* (again, excepting the special case of the sphenotic involved in the great broadening of the top of the cranium in *annulatus* and, especially, *formosus*).

The strong anterolateral frontal-sphenotic process at the rear of the orbit in *S. hyperostosis* leaves less of an open space over the eye between it and the lateral ethmoid than in any of the other species of *Sphoeroides* with a moderate interorbital width. In *S. hyperostosis* the distance between the rear edge of the extreme lateral end of the lateral ethmoid and the front of the anterolateral process of the frontal-sphenotic is about 5.0% SL (average for both sides; based on extrapolated 240 mm SL of holotype) or 78% of the interorbital width (=1.3 times into interorbital). By contrast, for example, this distance in the five largest (and therefore most comparable) specimens of *S. maculatus* examined (201–225 mm SL) averages 9.5% SL (range 8.2–10.1) or

162% of the interorbital width (=0.6 times into interorbital), and in six specimens of *S. pachygaster* (127–218 mm SL) averages 11.5% SL (range 10.8–12.4) or 138% of the interorbital width (=0.7 times into interorbital). In the fossil *S. jamestyleri*, the distance between the lateral ends of the lateral ethmoid and sphenotic is relatively great, 351% of the interorbital width (=0.3 times into interorbital) (this measurement cannot be given accurately as % SL because of distortion in the axial skeleton of the paratype, in which the skull is exposed in dorsal view and the interorbital can be measured).

In *S. hyperostosis* the frontal has a thickened ridge on its dorsal surface coursing from the rear of the orbit somewhat medially to about the anterior end of the supraoccipital, and then continuing posterolaterally around the main body of the supraoccipital to end as a short narrow posteriorly directed process over the upper end of the epiotic. In all other species of *Sphoeroides* with the exception of *S. pachygaster* the dorsal surface of the posterior region of the frontal is relatively flat and plain, although often with a deep concavity posterolaterally that is confluent with the depression between the lateral flanges of the sphenotic and pterotic. In many of these other species of *Sphoeroides*, including *S. maculatus*, the extreme posterolateral edge of the frontal protrudes out beyond the upper end of the epiotic and pterotic to form a short roof, especially laterally. In *S. pachygaster* the uniquely deeply sculptured surface of the frontal bears a ridge from the middle of the orbit that courses in a gentle curve to the lateral edge of the posterior end of the frontal, which projects posteriorly as a short but relatively broad roof over the upper surface of the epiotic. The projecting posterior end of the frontal that forms the roof in *S. hyperostosis* and *S. pachygaster* differs from that of other species of *Sphoeroides* in being directed primarily posteriorly rather than posterolaterally and in being associated with ridges running back from the orbital region, while

this roof in *S. pachygaster* is larger than in all of the other species.

In addition to its weak ossification, deep sculpturing on the dorsal surface, and extensive frontal shelf over the epiotic, there are several other specializations by which the skull of *S. pachygaster* differs from that of other species of *Sphoeroides*, including the complete loss of the rudiments of the dorsal roof of the myodome, the lateral expansion of the articular facet of the palatine, and the absence of teeth on the first pharyngobranchial. By contrast, *S. hyperostosis* has especially well-developed remnants of the dorsal roof of the myodome and a palatine articular facet of moderate width (the branchial arches are unknown). In addition to its more moderate interorbital width, *S. hyperostosis* differs from *S. pachygaster* by its greater maximum size; even though *S. pachygaster* is one of the largest species of *Sphoeroides*, reaching a maximum size of 218 mm SL (USNM 42143, slightly longer than the 208 mm SL maximum size recorded by Shipp 1974:50–51), it is only about half the maximum length of *S. hyperostosis*. None of the contrasting features of *S. hyperostosis* and *S. pachygaster* can be attributed to size differences, including the hyperostosis that is the norm in *S. hyperostosis* throughout its size range of about 80 to 500 mm SL.

The extant *Sphoeroides* are all shallow water in-shore species that usually occur in depths less than 35 m, with the single exception of *S. pachygaster*, which usually is found in waters deeper than 100 m. The Pliocene *S. hyperostosis*, occurring in waters estimated to be between 50 and 80 m depth (Gibson 1967), has a depth distribution intermediate between that of *S. pachygaster* and all of the other extant species of *Sphoeroides*. The depth of the habitat of the Miocene *S. jamestyleri* has not yet been estimated but it was probably at least as deep as that of *S. pachygaster* and *S. hyperostosis* because the mesopelagic stomiiform *Vinciguerrria merklini* Danilchen-

ko is by far the most commonly preserved fish in the same Miocene deposits (Bannikov 1990:76).

Relationships

In each of the three most distinctive features of its skull *S. hyperostosis* exhibits some similarity with *S. pachygaster* alone among the 18 extant and the only other fossil species of *Sphoeroides*: (1) the lateral ethmoid with a broad upper surface without an obliquely sloping anterior edge (*hyperostosis*) or with only a slightly sloping anterior edge (*pachygaster*); (2) the posterodorsal region of the orbit roofed over by a strong anterolaterally directed process of the frontals and sphenotics (*hyperostosis*) or by a broader shelf from a lateral expansion of the frontal and an anterolateral extension of the sphenotic (*pachygaster*); and (3) the frontal with ridges from the orbital region extending onto a narrow (*hyperostosis*) to relatively broad (*pachygaster*) posteriorly directed expansion as a short shelf over the upper region of the epiotic.

Since these features do not occur in any of the other species of *Sphoeroides* or in species of other genera whose skulls are generally similar to that of *Sphoeroides* (the group of six genera to which *Sphoeroides* is allied, as characterized by Tyler & Paxton 1979), we are confident that these are specializations indicating that *S. hyperostosis* and *S. pachygaster* are each others closest relatives. The difference in the width of the interorbital in *S. hyperostosis* (6.3% SL) and *S. pachygaster* (7.0–9.7, average 8.4% SL) is not as significant as their shared specialized features. With less assurity we believe that the overall similarity of the skull of *S. hyperostosis* with that of *S. maculatus* and *S. parvus*, including the width of the interorbital, is suggestive of a relationship of *S. hyperostosis* and *S. pachygaster* with the complex of four species that includes *S. maculatus*, *S. parvus*, *S. tyleri* and *S. nephelus* as delimited by Shipp (1974). Figure 8 shows

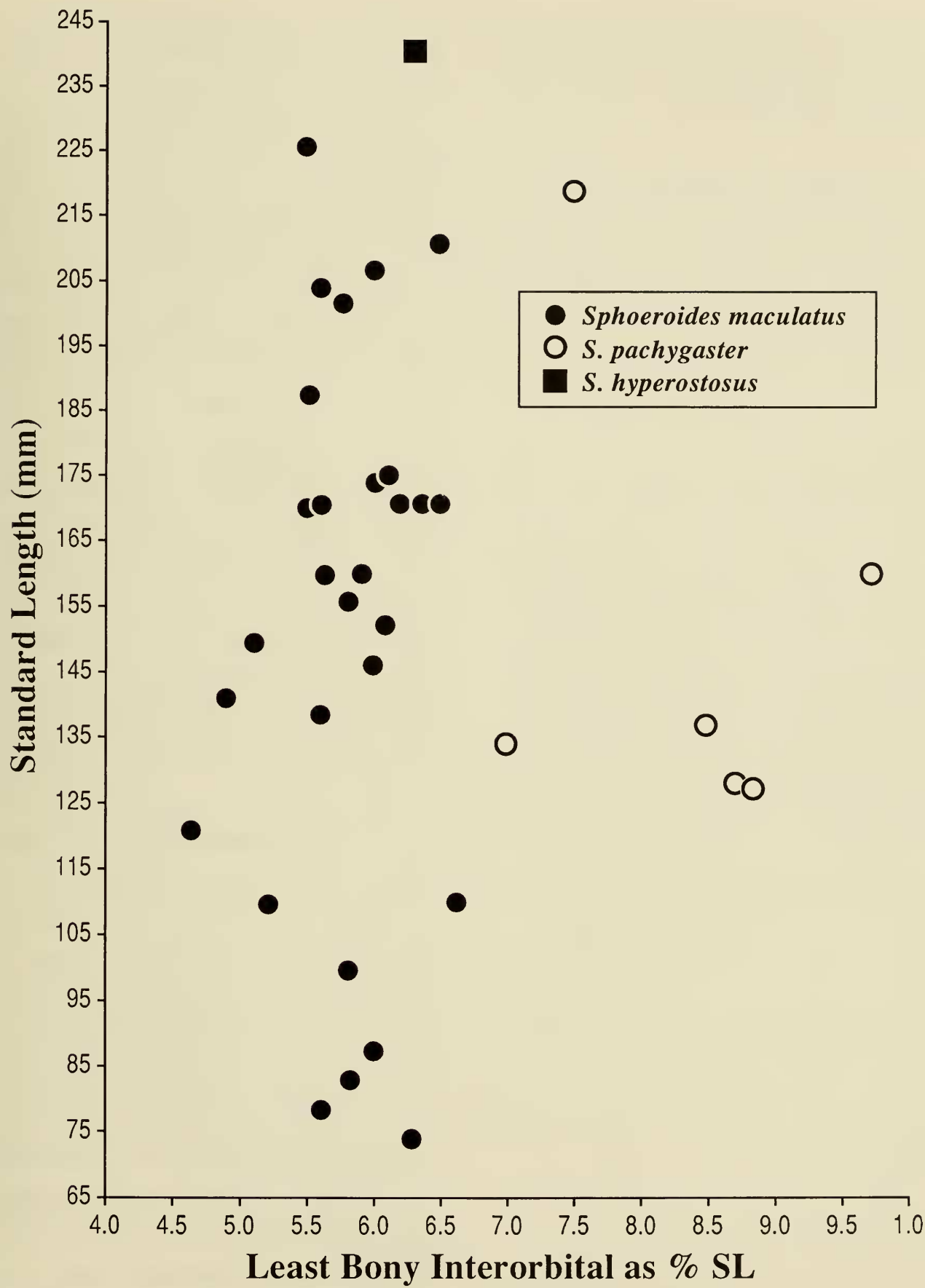


Fig. 8. Comparison of interorbital width between *Sphoeroides hyperostosis* and *S. pachygaster* and a representative (*S. maculatus*) of the species complex to which they may be most closely related.

the relative width of the interorbital, and its constancy with increasing specimen size in adults, of *S. hyperostosis*, *S. pachygaster*, and *S. maculatus*.

Hyperostosis in the Tetraodontidae

Hyperostosis has been found previously in only two genera of tetraodontids: in four species of *Lagocephalus* and in the monotypic *Xenopterus*. Abe (1960:406) and Abe et al. (1984:2) reported that the neural and haemal spines of some of the vertebrae in the caudal peduncle in *L. lunaris* and *L. spadiceus* are hyperostotic, whereas the lateral ethmoid, preopercle, and ventral postcleithrum are hyperostotic in *L. lunaris* but not in *L. spadiceus*. Abe & Tabeta (1983:5) also found that the neural and haemal spines of two of the vertebrae of the caudal peduncle (usually those of the 14th and 15th, but sometimes of the 13th and 16th vertebrae), the anterior end of the cranium (presumably ethmoid region) and the postcleithrum (dorsal or ventral not specified) of *L. gloveri* are hyperostotic in the majority of preserved specimens (205–320 mm SL) but apparently not in smaller specimens. Tyler (1980:268, 273, 323) reported that the ethmoid and the haemal spines of the 6th and 7th caudal vertebrae of *L. laevigatus* are hyperostotic in large specimens, but that the neural spines in this region of the caudal peduncle are not hyperostotic. We report here that in the single large specimen of *L. inermis* examined for this work (see Materials) the ethmoid and the haemal spines of the 6th, 7th, and 8th caudal vertebrae and the neural spine of the 7th caudal vertebra are hyperostotic.

Tyler (1980:340) reported that the frontals and the neural and haemal spines of the penultimate vertebra are hyperostotic in *Xenopterus naritus*. *Xenopterus* is one of the most specialized tetraodontids, with long-based dorsal and anal fins, an increased number of vertebrae and an open sac nasal apparatus. It is not considered to be closely

related to *Lagocephalus*, and the development of hyperostosis in *Xenopterus* and *Lagocephalus* must be independent.

We have examined hundreds of radiographs and cleared and stained specimens of the majority of extant species of tetraodontids in conjunction with previous research on the group (skeletal materials as listed in Tyler 1980:395–397; and the radiographs that were used to obtain most of the vertebral data in table 2 of that work) and have found hyperostosis only in those species of *Lagocephalus* and *Xenopterus* cited above. For the present study, we have radiographed a series of the largest specimens of *S. pachygaster* and *S. maculatus* available to us (see Materials) to explore the possibility that only especially large individuals of those species may develop hyperostosis, but none of these large specimens was found to exhibit this condition.

Hyperostosis is found almost exclusively among marine fishes. In the only well-documented example of hyperostosis in a non-marine fish, that of the Miocene cyprinodontid *Aphanius crassicaudus* (Agassiz), it has been postulated by Gaudant (1978, 1979), Meunier & Gaudant (1987), and Landini & Sorbini (1989) that the development of this hyperostotic condition is caused by fluctuations in the salt content of evaporating shallow bodies of water over gypsum (hydrous calcium sulfate) beds that become temporarily cut off from the sea. While the link between hyperostosis and extreme environmental conditions is well substantiated in that euryhaline species, the habitat of *S. hyperostosis* was normal coastal marine waters of about 50 to 80 m depth, and nothing associated with its habitat could reasonably be proposed as an abnormal condition that might in some way cause hyperostosis.

Hyperostosis is not known to occur to any unusual degree in the specimens of fishes from Lee Creek; the fish species from that formation that exhibit hyperostosis are the same as those that exhibit it in extant groups,

i.e., some ehippiids, carangids, gadids, etc. (based on manuscript by R. Purdy et al. describing the Lee Creek ichthyofauna). This, plus the fact that hyperostosis occurs in a wide size range of specimens (presumably over many generations and thousands of years of deposits) of *S. hyperostosis* and that without exception all of the thousands of disarticulated opercles, subopercles, preopercles, and ventral postcleithra that remain of the species are hyperostotic, leads to the reasonable conclusion that hyperostosis in *S. hyperostosis* is normal.

Acknowledgments

We are especially indebted to Craig Healy of Lexington, South Carolina, for his extraordinary and highly perceptive collecting efforts at Lee Creek Mine which resulted in the recovery of the first intact skull of a pufferfish and therein the solution to the mystery of the origin of the thousands of disarticulated hyperostotic bones from that formation. His generosity in donating this skull to the Smithsonian Institution is deeply appreciated.

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